Food Choice and Environment Occupancy in Afrotropical Dung Beetles: a Phylogenetic Study of two Examples (Coleoptera, Scarabaeidae)

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ABSTRACT

Phylogenetic studies of two genera of Afrotropical Scarabaeidae dung beetles (*Euoniticellus* and *Milichus*) have enabled to clarify some points in their evolutionary history. The species of *Euoniticellus* which have experienced an early separation from the rest of the genus live in forest and use non-ruminant mammals dung of the elephant type. Phylogenetic analyses enable to assume that the ancestor had the same macrohabitat and microhabitat. In the course of evolution, the genus seems to have gradually invaded savanna environments and ruminant mammals dung, when these new habitats were available. These changes considerably enlarged the genus' ecological niche. The genus *Milichus* experienced the same change in food, but the change in environment has been inverse and took place from savanna to forest.

RÉSUMÉ

Régime alimentaire et utilisation de l'environnement chez des coléoptères coprophages afrotropicaux : étude phylogénétique de deux exemples (Coleoptera, Scarabaeidae)

L'étude phylogénétique de deux genres de Scarabaeidae coprophages afrotropicaux (*Euoniticellus* et *Milichus*) a permis de préciser certains éléments de leur histoire évolutive. Pour ce qui est des *Euoniticellus*, les espèces qui se sont séparées précocement du reste du genre vivent dans des milieux de forêt et exploitent les déjections de mammifères non ruminants, du type de l'éléphant. La même analyse permet de penser que l'ancêtre du genre avait les mêmes macrohabitat et microhabitat. Dans le courant de l'évolution, le genre semble avoir envahi les milieux de savane et les excréments des mammifères ruminants au fur et à mesure que ces nouveaux habitats étaient disponibles. Ces changements ont considérablement agrandi la niche écologique du genre *Euoniticellus*. Le genre *Milichus* a connu le même changement de nourriture, mais son changement d'environnement s'est fait en sens inverse : de la savane vers la forêt.

INTRODUCTION

The present environments of tropical Africa can be divided into two well-defined and contrasted groups: tropical evergreen rainforest and both grasslands and woodlands, these two latter environments or biomes constituting the "savanna" category (especially in West Africa:

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GHAZANFAR, 1989). Most Afrotropical plants and animals live in either forest or savanna. This division is clear-cut, at least as far as Scarabaeidae dung beetles are concerned: no forest species inhabit savanna, and vice versa (CAMBEFORT, 1991c; CAMBEFORT & WALTER, 1991). However, most of the generally recognized genera (*i.e.* monophyletic ensembles of species – as far as phylogenetic studies have established their monophyly) comprise forest and savanna species. Therefore, in these monophyletic groups, some species must have changed from one environment to another. In each case, it can be asked which was the ancestral environment, and what was the influence of this change on the history of the genus.

The vegetal environment constitutes what could be called the "macrohabitat" of populations. Within these macrohabitats, the Scarabaeoidea lineage experienced changes in diet from a supposed mycophagy to such advanced diets as wood, flowers and dung (SCHOLTZ & CHOWN, 1995). So-called dung beetles live in and around the "microhabitats" made up by the excrements of animals, especially of mammals. Dung beetles also use these excrements as their food. Although these insects are able to accept different sorts of dung, they seem to have rather precise requirements for adult food, and especially for the making of brood balls which larvae eat from inside and develop in (CAMBEFORT & HANSKI, 1991). According to these preferences, it is possible to divide dung beetles into omnivore dung specialists and herbivore dung specialists. In this latter category, it is possible to distinguish between non-ruminant herbivore dung specialists and ruminant herbivore dung specialists (CAMBEFORT, 1984, 1991c; TRIBE, 1976). In the second case, most genera comprise both categories of specialists. In the course of each genus' history, changes in food (microhabitat) can have occurred, as well as in macrohabitat. Therefore, it can be asked how these changes have occurred, and what was their influence on the evolutionary history of the genus. To test this two-fold problem (changes in macro- and microhabitat), two genera of dung beetles have been selected: *Euoniticellus* and *Milichus*. Both are specialists of large mammals' dung. But some of their species occur in forest, some others in savanna; some species prefer the dung of Bovine mammals (including cattle), some others are found only in elephant dung.

MATERIAL AND METHODS

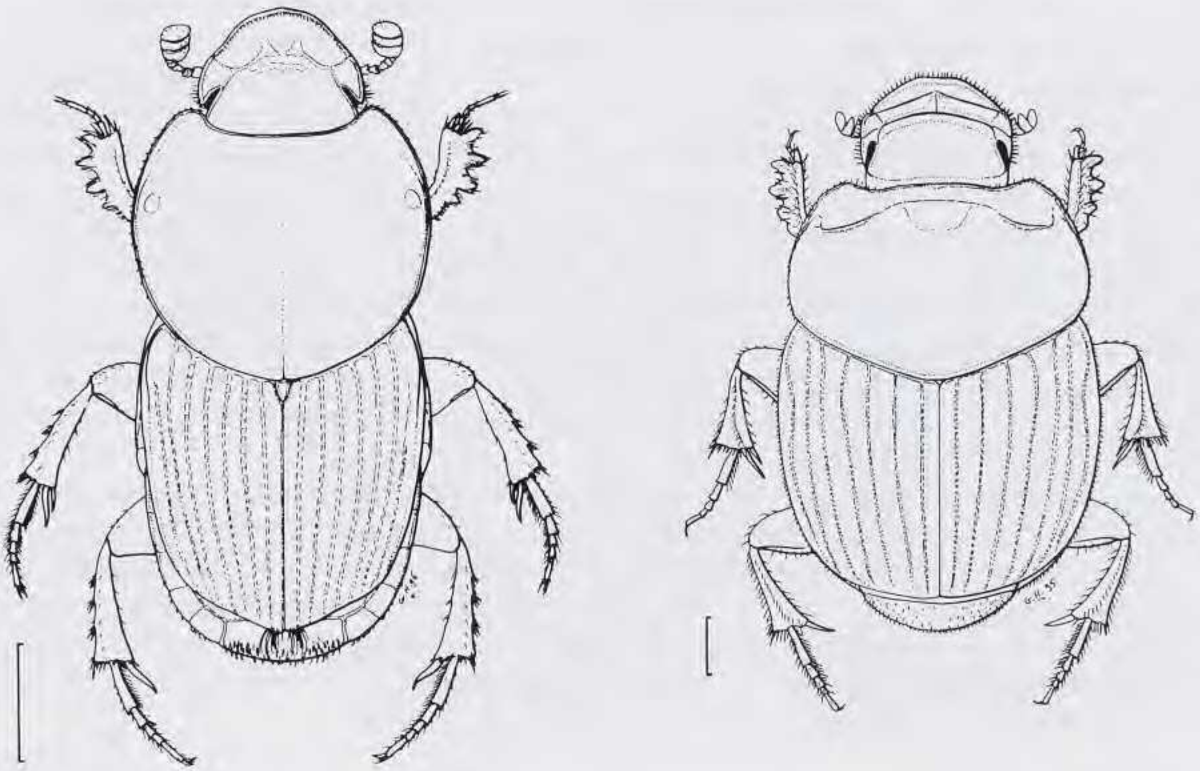
The taxa

Genus *Euoniticellus* Janssens, 1954: The 19 species of the genus (habitus: Fig. 1) occur mostly in tropical Africa (14 species). There are 2 species in the Palaearctic region, 2 in the Oriental region (including one in common with the Palaearctic region), and one Neotropical species, restricted to Cuba and Jamaica. These species are specialists of large herbivore mammals' dung, especially elephant and Bovini (including cattle). Some species are among the most evolved and efficient dung beetles, because they have developed optimal use of dung. Their larvae use the most nutritious part of this dung ("coprobiontic" alimentation: CAMBEFORT, 1991a), which allows the female to lay eggs a very short time after emergence (down to 5 days: HALFFTER & EDMONDS, 1982). A phylogenetic study of the genus, which will not be detailed here, has produced the cladogram of Figs 3-4 (CAMBEFORT, 1996b).

Genus *Milichus* Péringuey, 1901: The taxon (habitus: Fig. 2) is endemic of Afrotropical region. There are 15 described species, all specialists of herbivore mammals' dung, which live both in savanna and forest. As for *Euoniticellus*, a phylogenetic analysis of this genus has recently been published (CAMBEFORT, 1996a).

Habitat choice

Habitat (both macro- and microhabitat) choices are here considered as "attributes" of the relevant species (see following paragraph). These choices of most of the species of the genera *Euoniticellus* and *Milichus* have been established from field works, especially the author's ones (published or not), and according to other authors (*e.g.* KINGSTON, 1977). As for the environment (macrohabitat), there is no possible doubt: the species clearly occur either in forest or in savanna (grassland and/or woodland). Food (microhabitat) choice is sometimes less clear-cut. It has been considered that, when more than 90 %



FIGS 1-2. — *Euoniticellus* and *Milichus* : habitus. **1:** *E. capnus* Cambefort, 1996; **2:** *M. boucomonti* Cambefort, 1996. (Scale bars = 1 mm).

of the individuals occurred in either of the categories taken into account (elephant dung or cattle dung), the relevant species was a specialist of this sort of excrement (HANSKI & CAMBEFORT, 1991). When there was some doubt, the choice (the attribute) has been considered as polytypic.

Evolution of attributes

The ecological traits have not been used for establishment of the relevant phylogenies. These traits are not considered as characters but rather as attributes, according to the definition given by GRANDCOLAS *et al.* (1994): "an attribute is a trait of which primary homology is questionable, because it does not match the homology criteria; an attribute is empirically an extrinsic or widely defined trait; it is not used for phylogeny construction but is studied in reference to an independent phylogeny". For this reason, some consensus exists in favor of treating ecological aspects of the niche as attributes and not to use them to construct the tree whose aim is to clarify their changes (*e.g.* BROOKS & MACLENNAN, 1991).

For the present study, the program MacClade, version 3.04, was used. This program has a set of functions which enable the study of the analysis of characters, including traits not used to construct the tree (MADDISON & MADDISON, 1992, 1993). These functions use the classical principles of character optimization according to Fitch parsimony (*e.g.* KITCHING, 1992).

RESULTS

Genus Euoniticellus

The phylogenetic study of the genus (CAMBEFORT, 1996b) shows that it can be divided into two clusters of species: a paraphyletic cluster (from *perniger* to *parvus*), which comprises smaller species (average length: 5 mm); a monophyletic group (from *cubiensis* to *pallipes*), which comprises species whose average length is almost two times bigger (9.6 mm). The former cluster consists of species close to the tree root, and which, in this hypothesis of phylogeny, can be considered for this reason as "older". They occur mostly in tropical Africa, with one species in tropical Asia. In general, they are rare or very rare, with restricted geographical distribution, and most of them have been described rather recently. The latter group represent a monophyletic clade which consist of probably more recent species. They are more widespread than the former species, with a vast geographical distribution. Most of them have been described a longer time ago (XIXth or even XVIIIth century). Most of them occur in Tropical Africa, but some also occur in Palaearctic and/or Oriental regions, with one Neotropical species. These 11 species are the descendants of one ancestral species and constitute the sister-group of one species of the former group: *E. parvus*. The ancestral species split from the stem of the "older" species at some time during the evolution of the genus, and experienced an especially important cladogenesis which gave rise to a clade of eleven species.

On the relevant phylogeny, the ecological attributes have been mapped: food or microhabitat and environment or macrohabitat. There is a very clear difference between smaller and larger species as far as food is concerned (Fig. 3): while the former prefer elephant dung (only *E. parvus* occurs exclusively in cattle), most of the latter occur in cattle dung (only the twin species *E. kawanus-tibatensis* prefer elephant dung). The difference is also clear in the case of the environment (Fig. 4): most of the smaller, elephant specialist, basal species occur in forest; most of the larger, cattle specialist, apical species occur in savannas.

Genus Milichus

The phylogeny of this genus (CAMBEFORT, 1996a) does not show such clear-cut species groups as in the preceding case. Only the 4 species of the top of the tree, which form a monophyletic group (with two pairs: *dudleyae/dudleyi* and *inaequalis/lecourti*) are of a smaller size than the other species. In the same way as *Euoniticellus*, two ecological attributes have been studied: food and environment. As for food choice (Fig. 5), although it is unknown for 4 species out of 15, it seems clear that a mere minority of the species occurs in cattle dung (also 4 species out of 15). On the contrary, elephant dung seems to be the choice of 8 species. On the 15 described species, 10 live in herbaceous environments, grasslands and/or woodlands (Fig. 6). A mere 5 species occur in evergreen rainforest, of which 4 constitute a monophyletic group, and the 5th one seems to have diversified separately and specialized for this environment from a step living in humid savanna of the Guineo-Congolian type (GHAZANFAR, 1989).

DISCUSSION

The ecological attributes which have been reported on the phylogenetic hypotheses of the genera *Euoniticellus* and *Milichus* are recent. The past environments were probably not the same as the present ones. Also, it is difficult to know which sort of dung was used as food by the

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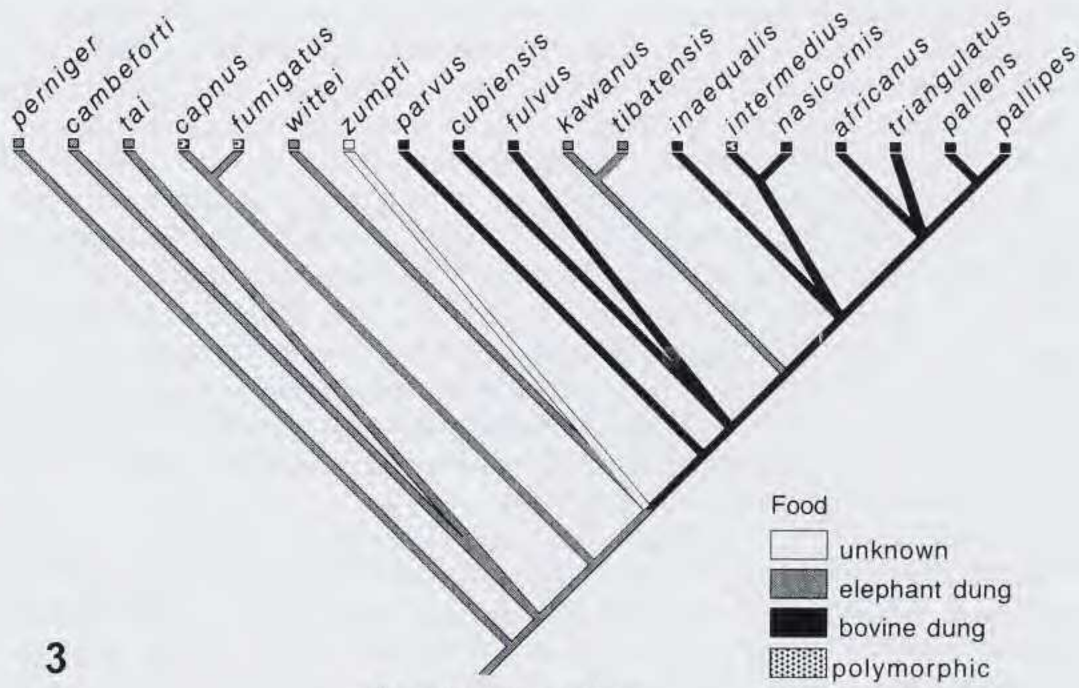
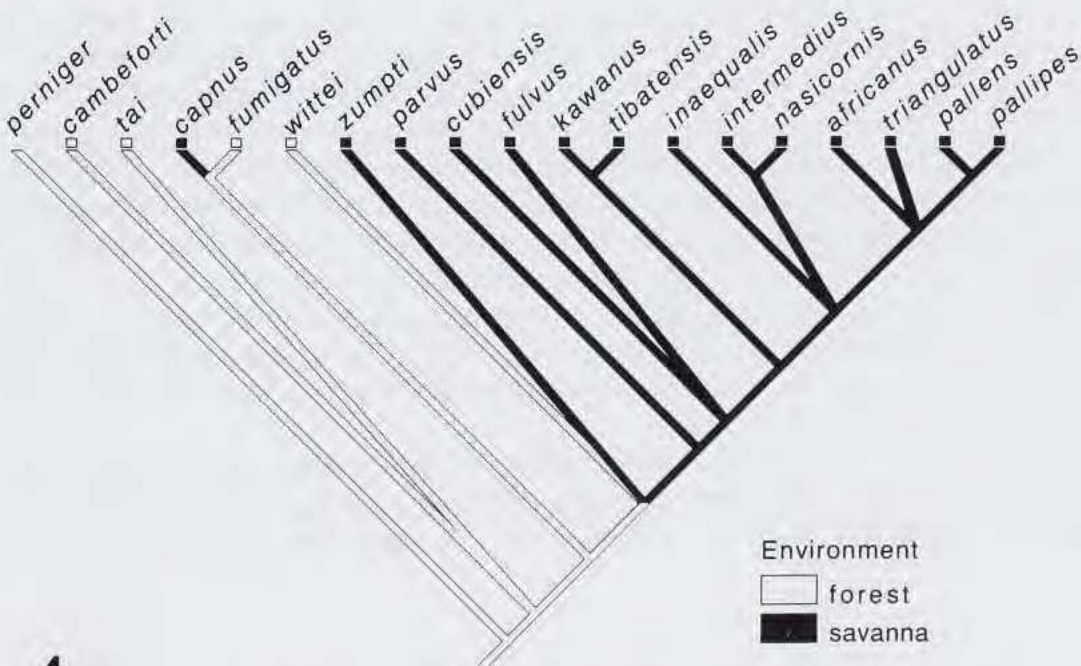
FIGS 3-4. — Phylogeny of the genus *Euoniticellus*, with ecological attributes optimized. **3:** food (microhabitat); **4:** environment (macrohabitat).



3

Euoniticellus : food



4

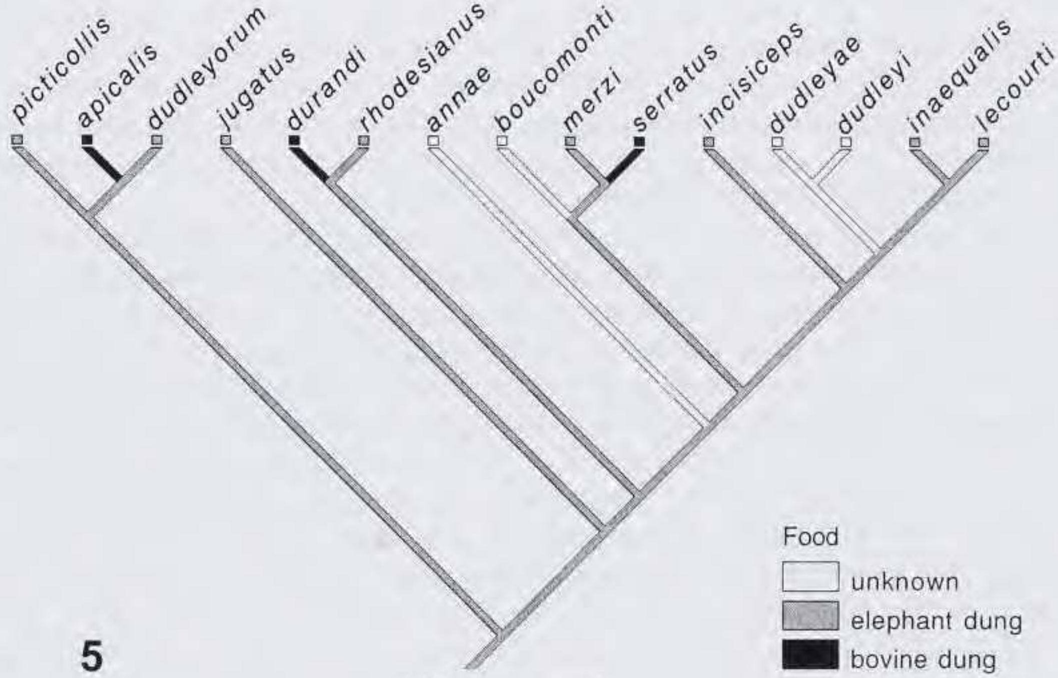
Euoniticellus : environment

ancestors of the living species. But I assume that, in the early history of the genus, both macro- and microhabitats were not very different from the present ones. In the phylogenetic tree of *Euoniticellus*, ecological attributes show a clear-cut change both in food and environment. Smaller, "primitive" species live(d) in forest environments and use(d) the dung of browser mammals of the type of the elephant's. These are coarse dung types, small parts of which only can be used by smaller dung beetles (TRIBE, 1976). At some time in the genus' history, one of these species seems to have changed this diet for some grazer mammal dung, probably a ruminant one. The question is open as to the time – in the genus' evolution – when this change took place. In the present species, there is a "small" one (*E. parvus*) which feeds on cattle dung. On the other hand, there is a pair of "large" species (*E. kawanus-tibatensis*) feeding on elephant dung. According to MacClade's optimization (Fig. 3), this change occurred before the differentiation of *E. parvus*, and the specialization of the pair *kawanus-tibatensis* is of secondary nature. In any case, this change was a very important innovation, which opened quite a new area (or "niche") to the genus, and made possible the cladogenesis which produced the more modern species of the genus. It is possible that this cladogenesis was an adaptive radiation, which took place to fill the new niche of grazer mammals' dung.

These grazers, perhaps ruminants, no longer lived in the forest. Food change of *Euoniticellus* coincided with environment change: part of the forest which has originally covered almost the whole tropical Africa, was gradually changed into savanna: woodlands in the more humid areas, grasslands in dryer ones. This new environment, rich in grasses of the family Graminaceae (Poaceae), induced the evolution of quite a new fauna of grazer mammals, among which the Bovini possess the most evolved digestive adaptations. Their dung has a very fine structure and allows an optimal use by dung beetles, both adults and larvae. The joint change in micro- and macrohabitat, which possibly occurred almost at the same time (at the geological scale), opened a new niche: ruminant-dung-in-savanna, which has been exploited by the *Euoniticellus* species ancestor of the group *cubiensis-pallipes*. This new niche has proven more successful than the older one (browser-dung-in-forest), enabling the adaptive radiation of modern *Euoniticellus*, which have occupied all the environments of savanna, and even gone out the tropical areas, probably following their mammalian sources of food. Moreover, cattle domestication by man even enlarged this niche and geographical distribution of the genus. Up to this point, the spreading of the taxon has been a natural one. Recently, the efficiency of some *Euoniticellus* in recycling cattle waste, having been taken into consideration, one species (*E. intermedius*) has been introduced artificially into Australia. It is now one of the most successful of the introduced species in this area (DOUBE *et al.*, 1991). The species has also been introduced into other Oceanian areas: New Caledonia and Vanuatu (GUTTIERREZ *et al.*, 1988), and also in (sub)tropical America (FINCHER, 1986).

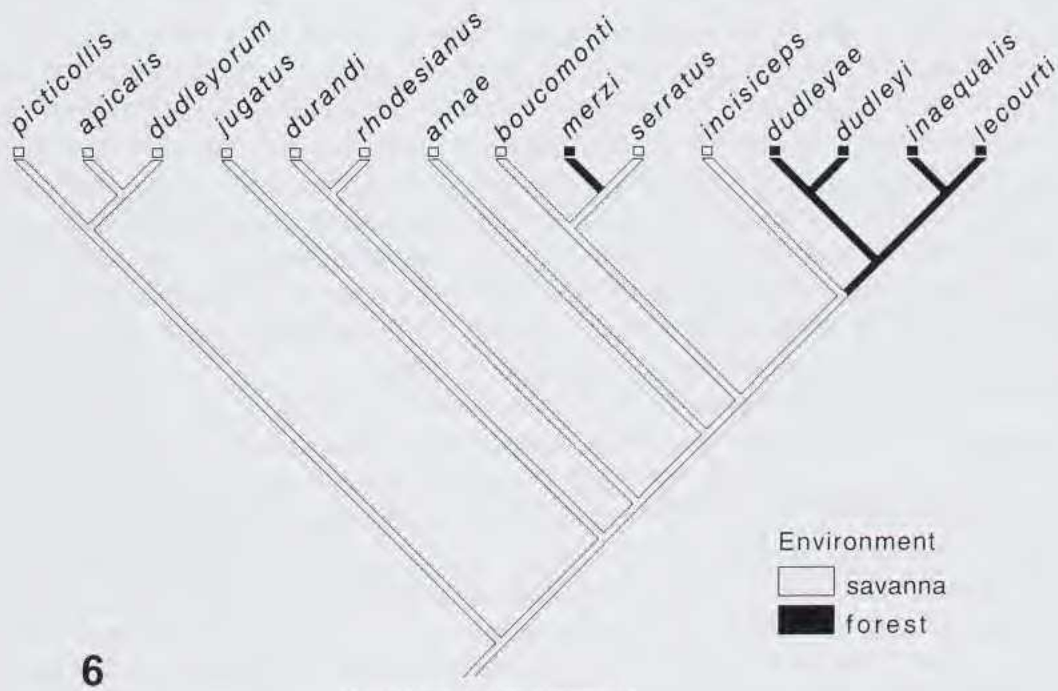
Coming back to the adaptive radiation of the modern species of *Euoniticellus*, it is worth remarking that their size is larger than for those using elephant dung. This is in contradiction with a previously established "rule" (*e.g.* CAMBEFORT, 1991c), according to which there is a

FIGS 5-6. — Phylogeny of the genus *Milichus*, with ecological attributes optimized. **5:** food (microhabitat); **6:** environment (macrohabitat).



5

Milichus : food



6

Milichus : environment

correlation between average size of mammals and of dung beetles using their dung. Now, this is a general rule, valid for the entire dung beetle fauna. In the case of the genus *Euoniticellus*, optimal utilization of cattle dung, which is highly characteristic of the genus, and higher alimentary value of this type of dung, possibly enabled the species having this diet to reach a larger average size than those exploiting elephant dung. On the contrary, size ratio in the genus agrees with another "rule" according to which savanna dung beetle species have an average size larger than forest species (CAMBEFORT & WALTER, 1991).

Is it possible to give a minimum date, even approximate, of the change of habitats that lead to the "modern" *Euoniticellus*? First pollen grains of grass appear, in Africa, in the mid-Eocene (VAN DER HAMMEN, 1983), documenting the first grassland and woodland areas. During the Cenozoic, grass formations evolved between forests and (sub)deserts, probably at the expense of the former, and at least to some extent owing to the action of "megaherbivores" (OWEN-SMITH, 1988), *i.e* large herbivorous mammals of the elephant type, which seem to have been abundant in Africa at least from Miocene to Holocene (KALB, 1995). Due to their action, arboreal vegetation disappeared on vast expanses of land, where grass was able to develop (CAMBEFORT, 1991b, 1991c). But it was for the benefit of other mammals: the so-called grazers, including ruminants, group of which the Bovini represent the more advanced branch. It is in the Pliocene that recent Bovini began to appear in Africa, probably from Asia (*e.g.* GENTRY, 1990, 1992; GERAADS, 1992; THOMAS, 1984; VRBA, 1985). It is from that time on that modern *Euoniticellus*, which may have begun to settle in woodland areas in large mammal dung (*cf.* the *E. kawanus-tibatensis* pair), must have started to use Bovini dung. More Bovini gained importance and number, more modern *Euoniticellus* became widespread, in Africa first, then in Asia, and finally in America, of which *E. cubiensis* is up to now the proof. Today, this species lives in grassland areas in Cuba and Jamaica, where it uses cattle pats (MATTHEWS, 1966). It is possible that its ancestors once followed Bovini troops during their migration eastward. As Bovini have never reached the West Indies, we must assume that this dung beetle has, for some reason, changed its diet and started to use the dung of some large American mammals: Edentata (Xenarthria) of the group of terrestrial sloths (Megalonychidae), for these were the only large mammals in Cuba (ITURRALDE-VINENT, 1988). The beetle then might have followed the mammals in their land or sea journey towards Large Antilles. Finally, the mammals disappeared there, and the beetle turned back to Bovini dung, when cattle was introduced into the islands, from XVIth century on. This is a rather complicated history, but the real "scenario" may have been even more complicated. In any case, the species is not very different from other "modern" *Euoniticellus*, and does not make a particular section in the genus (contrary to MATTHEWS, 1966).

All the precedent paragraphs dealt with *Euoniticellus*. If we now consider the genus *Milichus*, and first its microhabitat (food), it seems that there has been also a change from elephant ("old" species diet) to Bovini dung ("modern" species diet). In this case, change of macrohabitat seems to have been from savanna to forest. Africa occupancy by *Milichus* species seems to have been not "centrifugal" (*i.e.* from central forest to peripheral savannas, as in *Euoniticellus*) but centripetal (*i.e.* from savanna to forest). Now, centrifugal dispersion (in Africa) leads to a larger distribution than a centripetal one, due to the fact that the expanse of the savannas are larger than that of the forest, and used to be even larger because the relative extension of the forest versus savanna is now larger than average (MALEY, 1996). Older species of *Milichus* seem larger than more modern ones. These size relationships are less clear than in the precedent genus. Moreover, if the spreading really took place from savanna to forest, it is difficult to date it.

CONCLUSION

Study of evolution of two ecological attributes: food (microhabitat) and environment (macrohabitat) in two genera of Afrotropical dung beetles enables one to formulate some hypotheses concerning "evolutionary scenarios" of these genera. The shift from use of non-ruminant dung to ruminant (especially bovine) dung is assumed in the two cases in question. On the other hand, the shift from forest to savanna seems to have taken place in one case out of two. In any case, it is clear that those species whose evolution is in conformity with the double scenario: "non-ruminant dung → ruminant dung", and "forest → savanna" will be promoted by all means, including human action. This last factor in turn can act at two levels:

- passive action: destruction of Afrotropical forest and of elephant; multiplication and dissemination of domestic cattle;
- active action: introduction of dung beetle species into areas where they do not occur.

This is the case of some "modern" *Euoniticellus*, particularly of *E. intermedius*, which is now one of the most abundant and widespread dung beetle on earth. On the contrary, older species are "trapped" both in their macrohabitat and microhabitats. Coming back to the word "scenario", and giving it its proper meaning of "history", it could be said that the older species are not (or no longer) "in the sense of History". The scenario can even be expanded in the future, and it can be predicted – in the true meaning of the word, *i.e.* in the future – that the older species will get extinct before the more modern ones, and lamentably perhaps in a short span of time, together with the Afrotropical forest and elephant.

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